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COVER — A reconstruction of the terrain at the Port Kennedy, Pennsylvania, sinkhole that preserved a Late Irvingtonian fauna and flora. (See the paper by Daeschler, Spamer, and Parris in this volume.) Rendered by Bruce Mohn, Copyright © Bruce Mohn.

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Records of Musk Oxen from the Atlantic Coastal Plain of North America

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Introduction

RECORDS OF MUSK OXEN from the Atlantic Seaboard have been alleged for many years, at least since Allen (1876:12) commented that a deeply worn tooth from Pittston, Luzerne County, northeastern Pennsylvania, previously assigned to *Bison*, was "undoubtedly referable to the extinct musk-ox." Hay (1923: 248-249) reconsidered this tooth and concluded that it was ovibovine, possibly representing an undescribed taxon. We regard the specimen as an indeterminate bovid. A fragmentary horn core from Durham Cave, near Riegelsville, Bucks County, southeastern Pennsylvania, was described as *Bison appalachicolus* by Rhoads (1895), but we (Ray, 1966; McDonald and Ray, 1989a:25,67) regard it as a junior synonym of *Bootherium bombifrons*. Parris (1983: 13) considered the supposed "part of the scapula of a musk ox, *Bos moschatus*" collected at Trenton, New Jersey, in 1899 (Volk, 1911:111-112, 248-249; Plates 86 and 87, Fig. 1) to be indeterminate to family. The specimen could not be found in the collections of the Department of Anthropology, American Museum of Natural History, when Ray attempted to reexamine it in 1966, but the specimen represented in Volk's figure does not appear to be a scapula. In any case, the record cannot be sustained until or unless the bone can be restudied. The one allusion to musk ox in the Pleistocene of Florida (Neill, 1957:178) has been shown to be without material basis (Ray et al., 1963:393). Until the middle of the twentieth century, therefore, only one veritable record of a musk ox was known from the Atlantic Seaboard, that being the Durham Cave specimen from southeastern Pennsylvania—but until 1966 the affinities of even that specimen remained unclear.

During the second half of the twentieth century, however, several valid records of musk oxen from the Atlantic Seaboard have appeared. Three have been published upon previously (Whitmore et al., 1967; Parris, 1983; Ray, 1983; Gallagher et al., 1989), and *Bison appalachicolus* from Durham Cave has been properly referred to *Bootherium bombifrons* (McDonald and Ray, 1989a). In addition, four records have surfaced recently and have not been published upon. All seven of these records are from the Middle Atlantic Coastal Plain, including its seaward continuation as the Continental Shelf (Fig. 1). Both the extant tundra musk ox, *Ovibos moschatus*, and the extinct woodland or Harlan's musk ox, *Bootherium bombifrons*, are represented, and they extend the ranges of both species to the southeast. Along with a growing number of records of other boreal ungulates from this same region (McDonald and Ray, unpub. data), there is emerging a temporal and spatial pattern suggesting that the boreal megafaunal grazing community was present well onto the Coastal Plain of the Middle Atlantic region during glacial time.

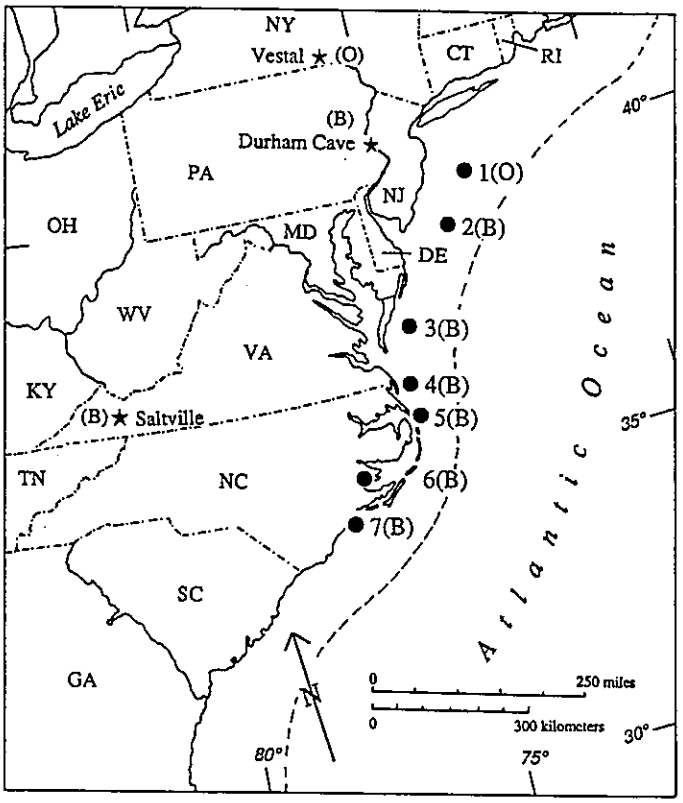

Figure 1. Middle Atlantic Seaboard of United States of America showing coastal plain localities for musk oxen. Numbers 1-7 correspond to numbered paragraphs in text. Parenthetical letters following numbers are O for *Ovibos* and B for *Bootherium*. Broken line offshore indicates approximate edge of continental shelf.

Our purpose here is to describe and summarize the valid records of musk oxen from the Atlantic Coastal Plain, to note the range extensions represented by these records, and to

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comment briefly upon the possible age and environmental affiliation of these musk oxen. The numbers preceding the specimens described below correspond with those appearing on Fig. 1.

Records of Musk Oxen from the Coastal Plain

Ovibos moschatus

1. USNM 392181 (Figs. 2-4).—A cranium of an adult male *Ovibos moschatus* was collected 20-60 miles (32-97 kilometers) offshore, and ca. 50-60 miles (80-97 kilometers) north of Cape May, New Jersey, by Sean MacCotter of Manahawken, New Jersey, while dredging scallops. Through an oversight on our part, this specimen was not included by Gallagher et al. (1989), and is reported here for the first time. The greater part of the cranium is preserved. Lacking are the distal 50 percent of the left horn core, the distal 60 percent of the right horn core, the frontals rostral to the horn cores, the basisphenoid, zygomatic processes, bony salients on the ventral side, and part of the medial part of the occiput dorsal to the foramen magnum.

The surface is coarsely pitted. The pattern of remaining bone is consistent with damage in high energy fluvial current. The edges, both natural and broken, are modestly rounded by abrasion by fine sediments transported in a fluid medium. A fresh break occurs across the rostral edge of the dorsal part of the cranium, indicating that this damage occurred during dredging.

The dorsal surface of the cranium is well preserved, with evidence of only relatively modest fine abrasion, and preserves the diagnostic morphology of a male of *Ovibos moschatus*—exostosis extending medially from the bases of the horn cores and nearly converging at the median. A narrow trough of smooth dense bone separates the exostotic surfaces. Measurements are presented in Table 1.

Bootherium bombifrons

2. PU 16340 (Figs. 5, 6).—A left horn core of a male of *Bootherium bombifrons*, about 80-90 percent complete, and the adjacent half of the dorsal part of the cranium was collected in 1950 by scallop dragger David Leeds. This specimen was collected from the continental shelf approximately 40 miles (64 kilometers) southeast of Atlantic City, New Jersey, at a depth of some 30 fathoms (55 meters). The specimen was donated to Princeton University by Carroll B. Atkinson. In 1985 the collection of fossil vertebrates at Princeton University was given to the Peabody Museum of Natural History, Yale University. The Princeton catalog numbers have been retained.

This specimen shows fresh damage to the distal tip of the horn core and the ventral side of the cranium. This damage could have taken place on two occasions, once before collection—where the surface is light cream in color and lightly polished—and once at the time of collection, where the surface is light gray brown and not polished. Much of the surface of this specimen retains very good preservation of surface detail. There is no evidence of extensive polishing by fine sedimentary abrasion.

This specimen has been reported on previously by Whitmore et al. (1967:1480), Parris (1983:13), and Gallagher et al. (1989:106); it was figured by Parris (1983, fig. 4). Measurements are given in Table 1.

3. USNM 23787 (Fig. 7).—A partial left mandibular ramus of *Bootherium bombifrons* was collected in May 1966 during dredging by the scalloper *Aloha*, captained by Magnus Isakssen. The specimen was collected 40 miles (64 kilometers) northeast of Cape Charles, Virginia, from a depth of 25 fathoms (46 meters) at geographic coordinates 37° 30' N, 74° 44' W. It consists of the body of the mandible, lacking the ascending ramus and the distal tip. Four teeth, p4-m3, remain. This specimen is identified as *Bootherium* on the basis of the large size of the hypsodont, selenodont teeth and their lacking [1] cementum, [2] accessory stylids on the lingual side external to the enamel wall between the hypoconids and protoconids, and [3] accessory internal fossettes within the dentine field at the juncture of the hypoconids and protoconids. These features differentiate the teeth typical of *Bootherium* from those typical of *Ovibos*, *Bison*, and the camelids of the late Quaternary.

The proximal and distal breaks appear to have occurred naturally and not during collection. The bone has split away from the cheek teeth longitudinally on both sides. The lingual side has been glued, the labial side remains detached and provides a clear view of the remaining teeth, including the roots within the alveolar zone. These longitudinal breaks probably occurred during or after recovery, as a result of rough treatment or drying and shrinkage, and the two missing teeth probably were lost at that time. The remaining teeth are undamaged.

The animal to which this mandible belonged was a full adult. The m3 is in full wear, but the third cusp had just reached that stage. There is much wear left on m1. Measurements of the teeth are given in Table 2. This specimen was alluded to by Whitmore et al. (1967) and by Ray et al. (1967:621).

4. USNM 437665 (Figs. 8, 9).—A partial cranium of a male of *Bootherium bombifrons* was dredged from the continental shelf at least five miles (eight km) offshore of Currituck, North Carolina, by Gordon Rippon. The specimen was received for the Smithsonian by David J. Bohaska on 26 September 1989, but had been recovered several years previously. This specimen consists of the proximal ca. 40 percent of the right horn core and adjacent ca. 25 percent of the cranium. The dorsal surface of the cranium between the base of the horn core and the midline is present, as is the right half of the caudal surface dorsal to the occiput. Essentially all of the lateral surface ventral to the base of the horn core is missing. The medial surface of the specimen is essentially planar and sagittal, indicating that the skull separated along the sagittal plane, which typically is weakly fused in musk oxen.

This specimen is mineralized. The ventral part was broken away, apparently at the time that it was collected, judging from the freshly broken surfaces. The entire specimen probably was broken into the right proximal horn core and adjacent one-quarter of the cranium in a high energy current, then lightly polished by finer sediments. This condition is especially apparent on the rostral and medial surfaces of the cranium and in the erosion of cancellous bone from the interior of the horn core which, in this specimen, is deeply hollowed out. In contrast, much fine detail is preserved on the caudal and ventral sides of the horn core and, to a lesser degree, on the remaining part of the caudal surface of the specimen, suggesting that it was lying with its caudal and ventral surfaces in matrix protected from abrasion by fine marine-transported sediment. The most extreme wear by fine sediment occurs on the rostral surface of the horn core and the rostral and rostromedial surfaces of the cranium. All of these factors suggest that the fine polishing took place with the specimen partly imbedded and partly exposed, rather than

Table 1. Measurements (in mm) of horn core dimensions of *Bootherium bombifrons* specimens mentioned in text.

Specimen	Circumference at Base	Rostrocaudal Diameter	Dorsoventral Diameter	Length of Horn Core[1]
PU 16340		107.0		((334))
USNM 347315				
USNM 437665	349	114.4	91.8	((168))
USNM 13694	390	143.5	93.8	
USNM 13695	375	124.0	106.2	

[1]Measured at center along dorsal surface.
Figure in single parentheses indicates an approximate measurement for the complete character. Figure in double parentheses indicates measurement provided for incomplete characters solely to indicate the amount of the character that remains.

Table 2. Measurements (in mm) of teeth of *Bootherium bombifrons* mentioned in text.

Specimen	$p4^1$	$m1^1$	$m2^1$	$m3^1$	$p4^2$	$m1^3$	$m2^3$	$m3^3$
USNM 437774	49.3							
USNM 23787	(24)	27.0	30.4	51.4	17.8	19.0	23.3	22.2

[1]Rostrocaudal length, at neck. [2]Maximum transverse breadth. [3]Transverse breadth, anterior cusp.
Measurements in single parentheses are approximate for the character.

with the entire specimen exposed equally. Corresponding to this pattern of abrasion is one of coloration in which the more polished/abraded surfaces are orange-brown and the less polished surfaces are black-brown, suggesting that the different parts of the cranium were in contact with (actively) oxidizing and (previously) reduced environments, respectively. Further supporting the conclusion that only part of this cranium was exposed to the aqueous environment is the fact that patches of the encrusting marine bryozoan *Hippoporina americana* (Verrill) adhere to the exposed orange-stained portion—including the sagittal surface, at least three of the exposed sinuses, and the endocranial surface—but not the darker portion. (*Hippoporina americana* presently occurs along the Atlantic Coast of North America from Maine to North Carolina; based on the presence of noncalcified tissue of some of the bryozoans, at least some of the individuals were living when the musk ox cranium was dredged up.)

The characteristic horn core and dorsal cranial surface typical of males are obvious. The entire preserved dorsal surface is covered with secondary exostotic bone, which rises to a ridge along the midline. This secondary bone forms a deposit more than 35 mm thick along its caudal edge above the occiput. The horn core is subrounded, being flat to moderately convex on the dorsal surface and rounded below. The ventralmost point of the base of the horn core is located about midway between the rostral and caudal edges of the core. The exposed medial edge reveals the large frontoparietal sinuses typical of *Bootherium*. The minimum thickness as preserved from the dorsal surface of the cranium to the dorsal surface of the endocranium is 62 mm.

The horn core in this specimen is one of the largest on record; the only specimens that we have examined that are larger are USNM 13694 and USNM 13695 from American Falls, Idaho (Table 1).

5. USNM 347315 (Figs. 10, 11).—A nearly complete cranium with the caudal ends (ca. 68 mm) of both nasal bones of a female of *Bootherium bombifrons* was found in the surf at Oregon Inlet, Dare County, North Carolina, by Mrs. Odessa Wasili. The cranium lacks only the zygomatic processes, minor chips along the edges of the occiput, and bony salients on the ventral side. The distal 30-50 percent of the right horn core, and the distal 40-70 percent of the left horn core, are missing.

The specimen is lightly mineralized. It has been broken in a pattern suggesting transport in a high energy fluvial current, and had been exposed to abrasion by fine sediments long enough for wear of the cancellous bone filling the horn cores to begin. Otherwise, there is no evidence of excessive abrasion by fine sediments, only light smoothing of sharp edges where breaks and naturally sharp angles occurred and perhaps a gentle sanding of the entire surface. Sanding did not greatly alter the surface detail.

This is the most nearly complete cranium of a female of *Bootherium bombifrons* yet described. The specimen includes more of the nasals than almost any representative of the species, thus providing rare insight into at least the caudal part of the nasals and contributing to impressions of their morphology which, being narrow (48.8 mm at the rostral end of the frontals) and apparently not arched longitudinally, confirms their being more like *Praeovibos*, their presumed ancestor, than *Ovibos*. The surface pattern of the nasofrontal suture line is that of a flat-bottomed V, unlike the W-shaped suture pattern that is typical of *Ovibos moschatus*. The occipital plane slopes markedly in a ventrocaudal direction

from the nuchal line, a condition that has been observed in several specimens of *Praeovibos*, rarely in *Bootherium*, and not at all in *Ovibos*. Measurements of this specimen are given in Table 1. It has been figured previously in Ray (1983) and McDonald and Ray (1989a, fig. 41).

The specimen was donated to the Smithsonian Institution on 6 December 1982 by Mrs. Ruth Ann Burgess through David Lee and Charles Potter.

6. USNM 437774 (Fig. 12).—A right m3 of *Bootherium bombifrons* was collected by William Harmatuk at the Superior Stone Company (now Martin Marietta) Quarry, New Bern, Craven County, North Carolina. This specimen was received at the Smithsonian Institution 22 May 1988, but was collected a few years earlier. The crown of this tooth is complete, except for minor chips, and measures 50.5 mm in rostrocaudal length at the occlusal surface and 49.3 mm in length at the neck. The roots are largely broken away. The tooth was in full use at the time of death, but not deeply worn; the crown height is ca. 43.5 mm. Pleistocene land mammal remains are found at this locality in disturbed overburden thought to represent fluvial deposits, probably bed load of former stream channels.

7. USNM 336108 (Fig. 13).—A partial lumbar vertebra of *Bootherium bombifrons* was collected at Onslow Beach, Onslow County, North Carolina, by Mr. and Mrs. George A. Potter, who donated it to the Smithsonian Institution on 10 February 1982. This is a fifth lumbar vertebra consisting of the body and proximal part of the dorsal arch. Except for chipped edges and extremities, the prezygapophyses and postzygapophyses and the articular surfaces are complete. The transverse processes and dorsal part of the spine are missing. The caudal articular surface is relatively broader then the cranial surface. The specimen is extensively mineralized.

This vertebra is identified as ovibovine because of its ponderous body, relatively small neural canal, and weakly developed ventral keel. It is assigned to *Bootherium* because of its great size, being larger than most known for *Ovibos*, and its provenience from a site well south of the known range of *Ovibos*. Measurements are given in Table 3.

Table 3. Measurements (in mm) of USNM 336108, fifth lumbar vertebra of *Bootherium bombifrons* from Onslow Beach, Onslow County, North Carolina.

Length of body (PL)	63.8
Breadth of body across cranial end (BFcr)	77.0
Breadth of body across caudal end (BFcd)	80.0
Breadth across prezygapophyses (BPacr)	91.6
Breadth across postzygapophyses (BPacd)	68.5

Symbols in parentheses correspond to measurements defined in von den Driesch (1976).

Discussion

The records described above extend the ranges of both *Ovibos moschatus* and *Bootherium bombifrons* to the southeast of the previous known limits of distribution (Fig. 1). The cranium of *Ovibos moschatus* from offshore of Cape May, New Jersey, represents an extension of distribution for veritable *Ovibos* of some 250 miles (400 kilometers) south-southeast of the nearest previous record, a cranium from Vestal, Broome County, New York (Kitts, 1953). The only legitimate record of *Ovibos* in North America found farther south than the Cape May cranium is that from Reading, Hamilton County, Ohio (McDonald and Davis, 1989:1161).

When Ray referred the holotype of *Bison appalachicolus* from Durham Cave, Pennsylvania, to *Bootherium* (Ray, 1966), that specimen represented the easternmost occurrence of the genus. In 1967, the range of *Bootherium* was extended southeastward from central Kentucky (see McDonald and Ray, 1989a, figs. 63, 64) when cranial and postcranial elements were described from Saltville, southwestern Virginia (Ray et al., 1967). The extension of the range of *Bootherium* eastward and southward continued with reports of the mandible from off Cape Charles, Virginia (Whitmore et al., 1967) and the cranium from Oregon Inlet, North Carolina (Ray, 1983). The lumbar vertebra from Onslow Beach, North Carolina (USNM 336108), described for the first time in the present paper constitutes the most southeasterly record of the genus—an extension of some 100 miles (160 kilometers) south of the Oregon Inlet record.

Most of the records of musk oxen from the Coastal Plain almost certainly date from a glacial stage of the late Quaternary, probably the Wisconsinan, although we caution that this has not been demonstrated unequivocally by radiocarbon dating or other, strongly supportive circumstantial evidence. The fossil record and historic ecological data strongly support the view that *Ovibos moschatus* is closely affiliated with tundra or tundra-margin environments (McDonald and Davis, 1989; McDonald et al., 1991), whereas the other musk oxen known from North America—*Bootherium bombifrons* and three species of *Praeovibos*—were more eurytopic (Crégut-Bonnoure, 1984; Skwara and Walker, 1989; McDonald et al., 1991). Also, most specimens described in this paper show no evidence of having been transported far after death of the animal or of having been subjected to extensive or repetitive episodes of weathering or abrasion. Lastly, Whitmore et al. (1967) pointed out that the present surface of the Continental Shelf is no older than the Wisconsinan glaciation. The conclusion is reached, therefore, that the records of musk oxen from the Continental Shelf indicate occupation of the Shelf by musk oxen during, probably, the marine regression corresponding to the Wisconsinan glaciation.

The extreme southern record of *Ovibos moschatus* from off the coast of New Jersey almost certainly dates from the most recent glacial maximum based on the narrow ecological requirements of this tundra-adapted musk ox and its presence on the Continental Shelf only some 100 miles (160 kilometers) south of the southernmost margin of the ice sheet (Mickelson et al., 1983). The fact that four of the five records of *Bootherium bombifrons* from the Coastal Plain have been found either on the Continental Shelf or in the surf along the Atlantic Coast indicates that this species occupied the region during a glacial stage. *Bootherium bombifrons* might, however, have lingered in the region until near the end of the Pleistocene, well after the glacial maximum of about 18 ka, based on the presence of bones and teeth of this species at Saltville, Virginia, in sediments dated at between 13.5 and 10.0 ka (McDonald, 1990). As recent as 14.0 ka, most of the Continental Shelf of today, in the Middle Atlantic region, was emergent, a result of little melting of the Laurentide ice sheet prior to that time, and even by 9.5 ka the coastline was still east of its present location (Hughes, 1987; Ruddiman, 1987; Riggs and Belknap, 1988).

The increasing resolution of the late Quaternary range of *Bootherium bombifrons* and other large boreal ungulates in the eastern part of the United States (McDonald and Ray, unpub. data) is producing a pattern of distribution for this suite of herbivores that allows recognition of a southeastward extension of the "*Symbos-Cervalces*" faunal province of Martin and Hoffmann (1987). The extension of this province corresponds well with habitat described as being generally open boreal woodland, unstable and patchy, from the late Wisconsinan glacial maximum until after 15.0 ka, and perhaps even until about 10.5 ka (Delcourt and Delcourt, 1986; Jacobson et al., 1987; Webb et al., 1987). On the Coastal Plain, climatic conditions were cold and dry, occasioned by the rainshadow of the Appalachian Mountains, the southward penetration of effects of the Labrador Current, and the associated seasonal patterns of surface winds (Delcourt and Delcourt, 1986; Kutzbach, 1987). Aeolian processes, especially erosion and dune formation, might have contributed to the instability and patchiness of vegetation. Vegetation was also probably kept in disequilibrium by the effect of large browsing herbivores, such as ground sloths, mastodons, and mammoths (Whitmore et al., 1967; J.N. McDonald and Ray, 1989b; H.G. McDonald and Ray, 1990).

Musk oxen have been especially prominent in forming images of paleoclimates, in view of the tundra connotation of the only extant form, *Ovibos moschatus*. Such an image seems to be a valid assumption for *Ovibos*, but assuredly is not valid for *Bootherium*. Caution must be exercised, therefore, in extending current images of social characteristics and ecological affiliations to extinct taxa that are closely related to modern forms. Equal caution must be exercised in projecting current images of social and ecological characteristics of extant taxa to their earlier representatives.

Acknowledgments

We thank especially all of the collectors and donors noted in the accounts of individual specimens. Without them there would be no scientific record of ovibovines from the Atlantic Coast. Dr. Alan H. Cheetham, Department of Paleobiology, National Museum of Natural History, identified the bryozoans adhering to USNM 437665.

The photographs in Figs. 2-13 were taken by Victor E. Krantz. The photographic figures were prepared by David J. Bohaska with the aid of Mary Parrish. Fig. 1 was prepared by Mary Parrish with the aid of David J. Bohaska.

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Figures 2-13 follow.

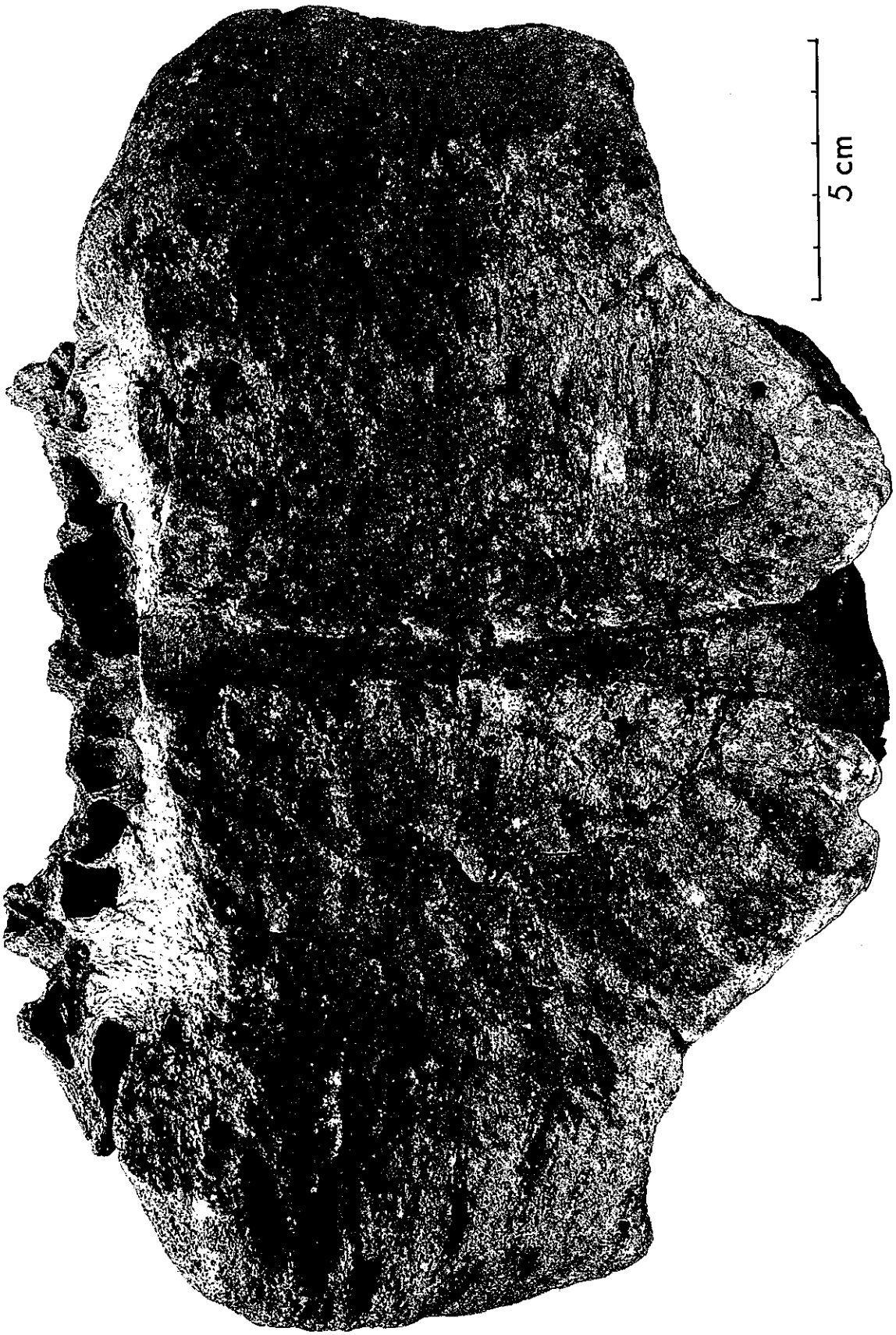

Figure 2. *Ovibos moschatus* cranium, male (USNM 392181), dredged northeast of Cape May, New Jersey; dorsal aspect.

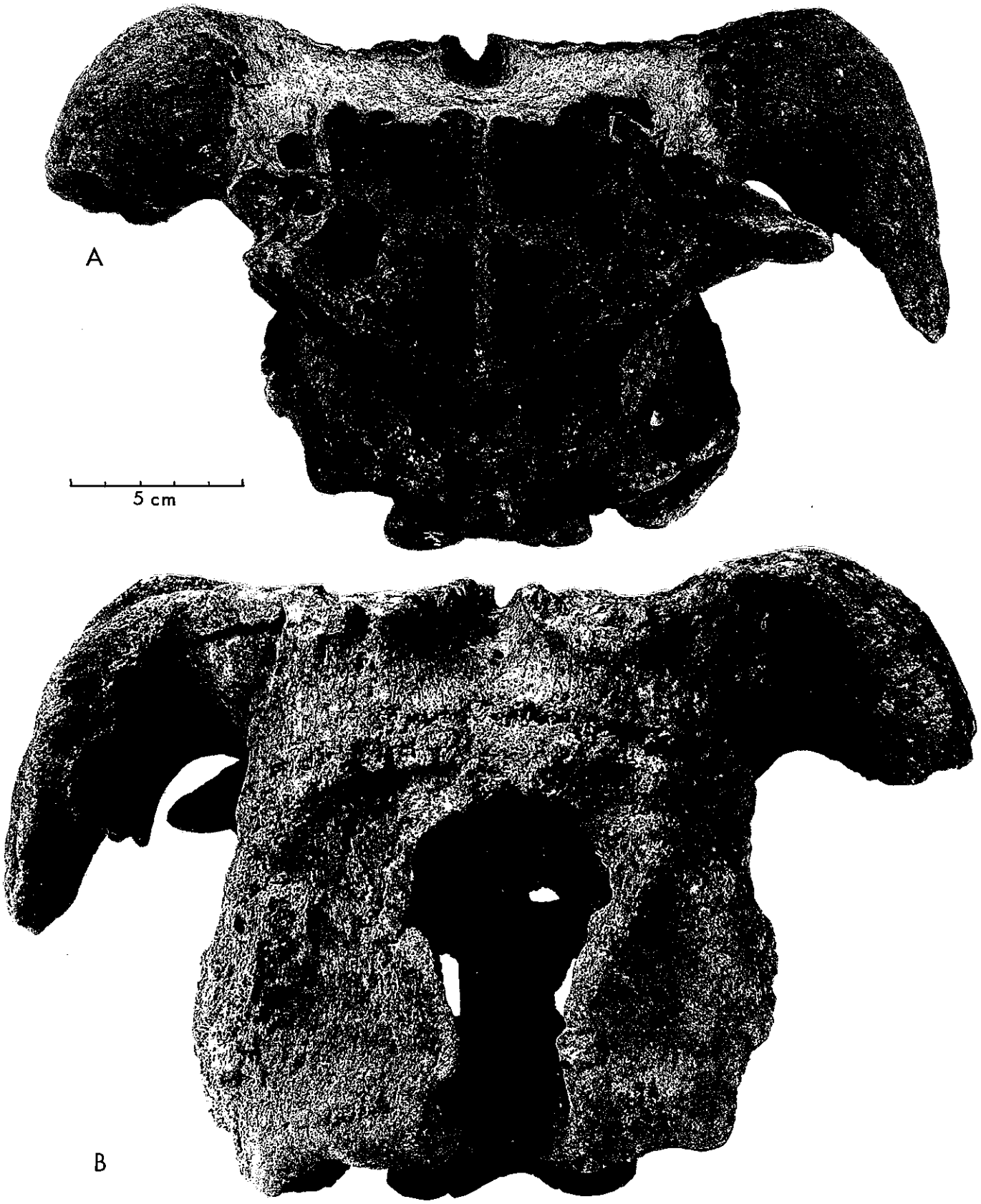

Figure 3. *Ovibos moschatus* cranium, male (USNM 392181), dredged northeast of Cape May, New Jersey; A, rostral aspect, B, caudal aspect.

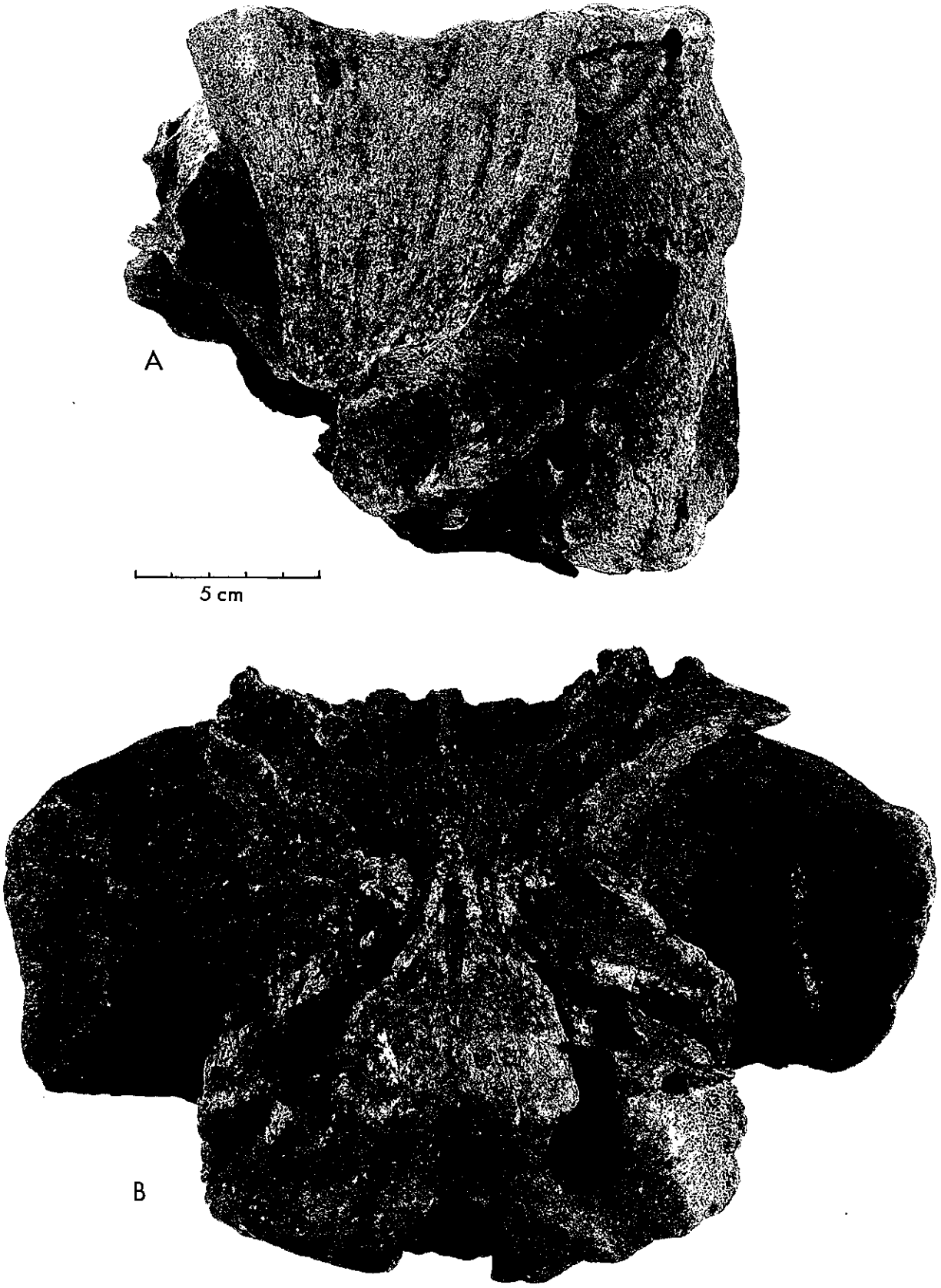

Figure 4. *Ovibos moschatus* cranium, male (USNM 392181), dredged northeast of Cape May, New Jersey; A, left lateral aspect, B, ventral aspect.

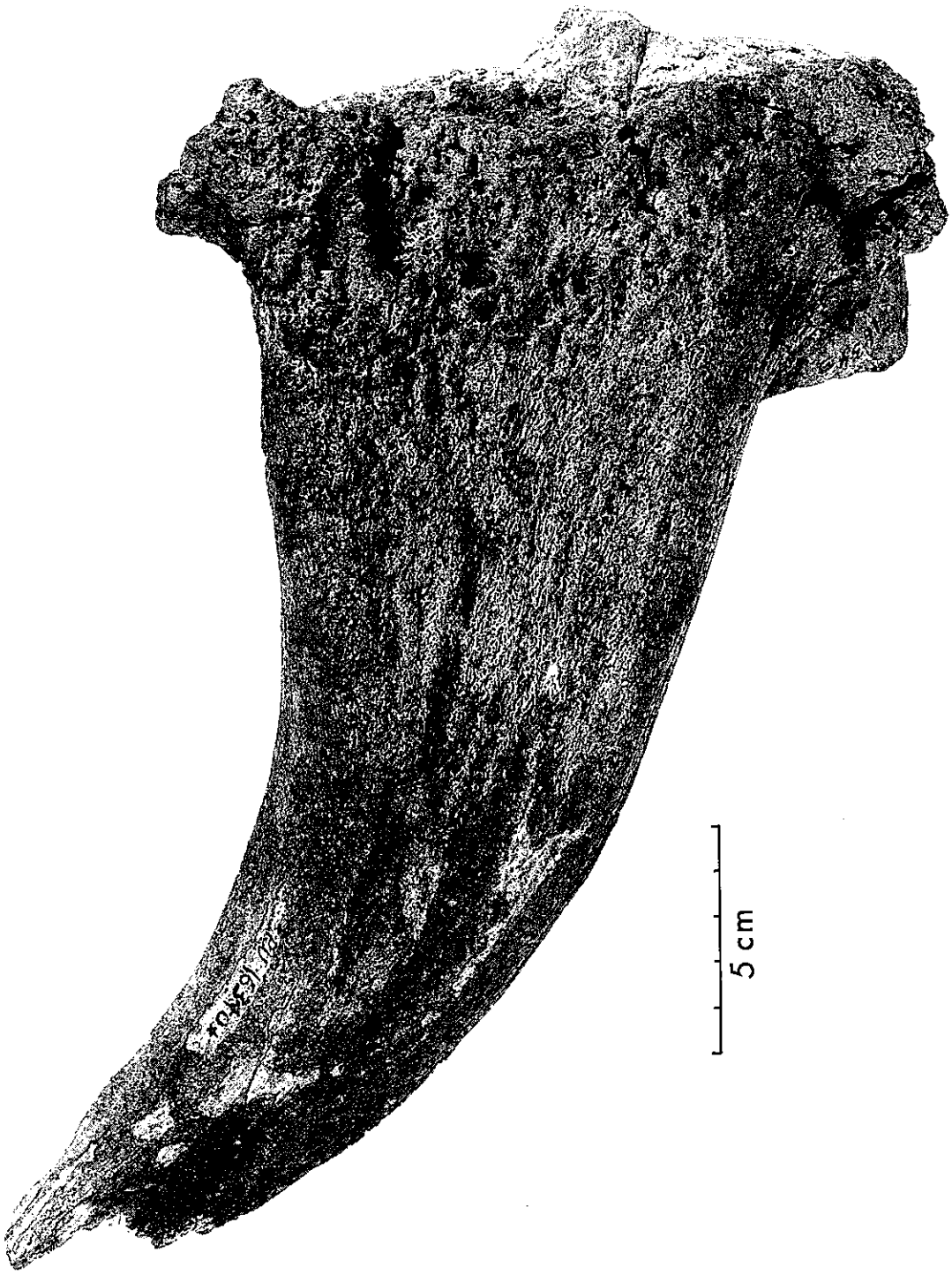

Figure 5. *Bootherium bombifrons* left horn core, male (PU 16340), dredged southeast of Atlantic City, New Jersey; dorsal aspect.

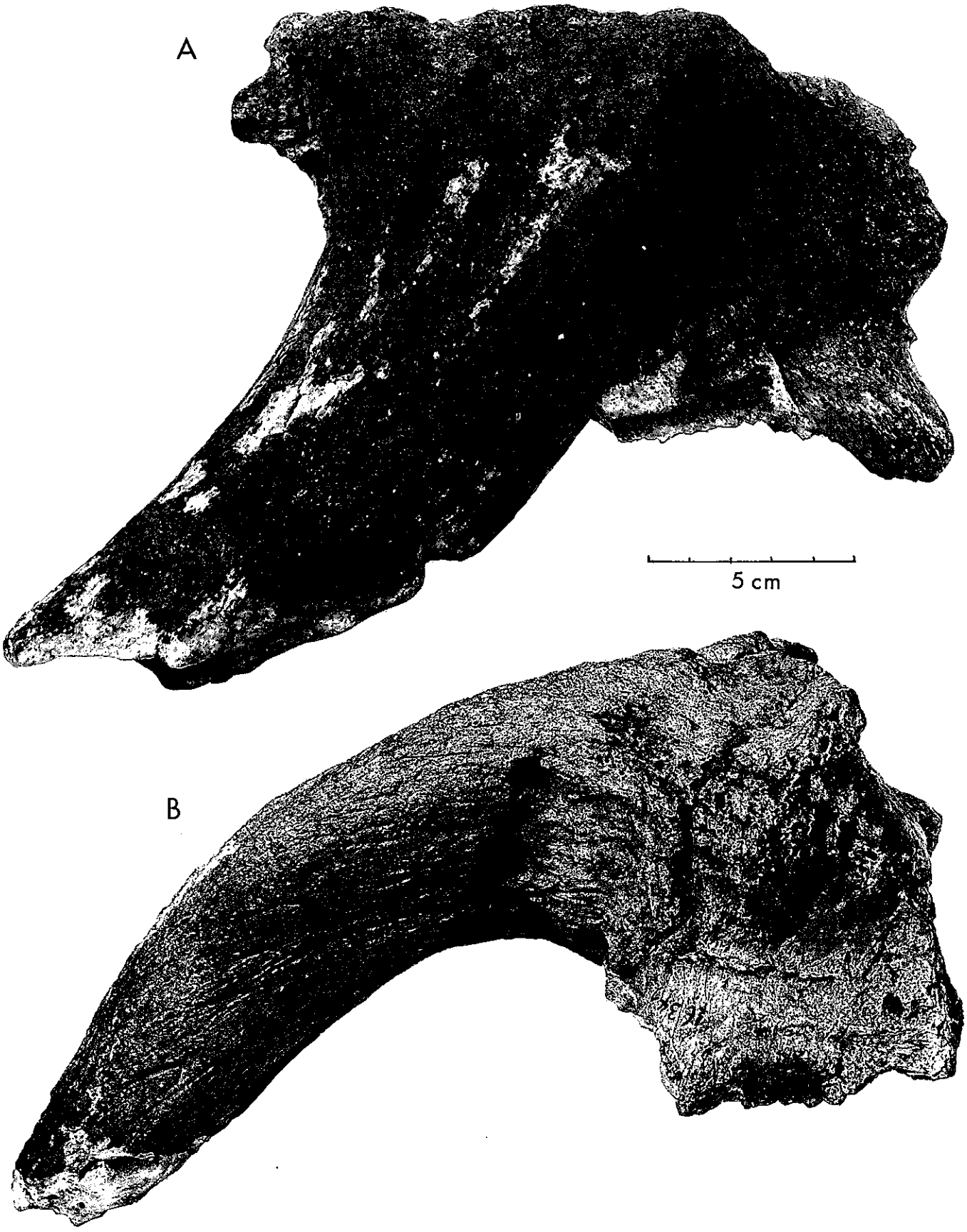

Figure 6. *Bootherium bombifrons* left horn core, male (PU 16340), dredged southeast of Atlantic City, New Jersey; A, left lateral aspect, B, caudal aspect.

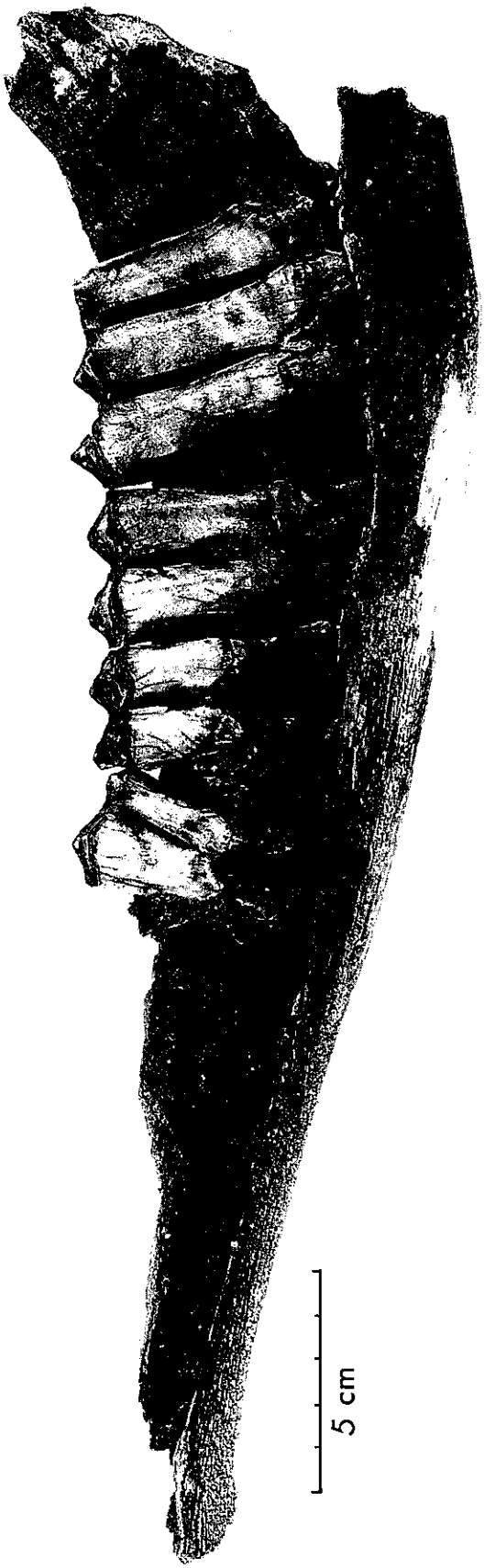

Figure 7. *Bootherium bombifrons* left mandibular ramus (USNM 23787), dredged northeast of Cape Charles, Virginia; labial aspect, with bone removed to show cheekteeth.

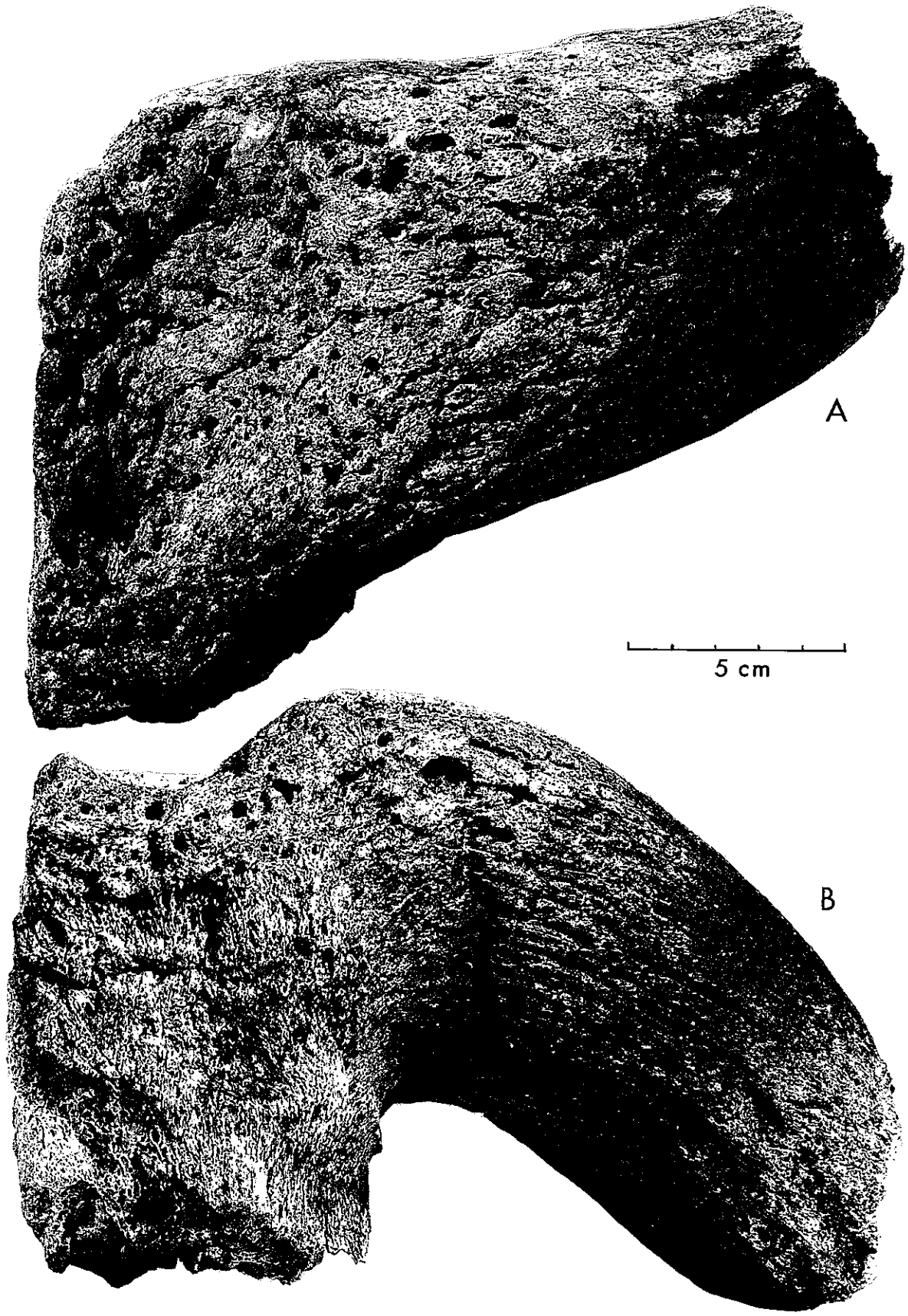

Figure 8. *Bootherium bombifrons* cranial fragment with right horn core, male (USNM 437665), dredged east of Currituck, North Carolina; A, dorsal aspect, B, caudal aspect.

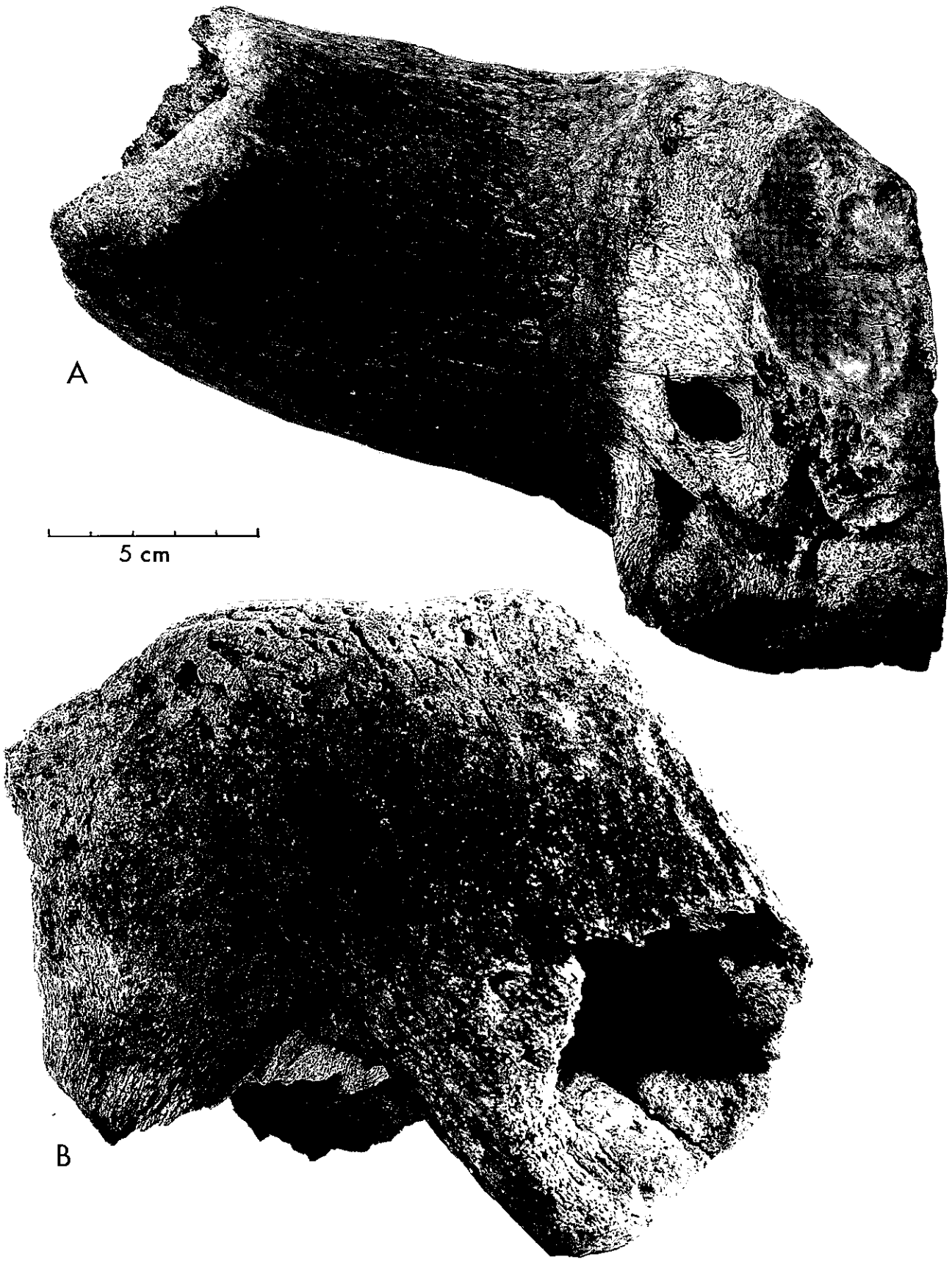

Figure 9. *Bootherium bombifrons* cranial fragment with right horn core, male (USNM 437665), dredged east of Currituck, North Carolina; A, ventral aspect, B, right lateral aspect.

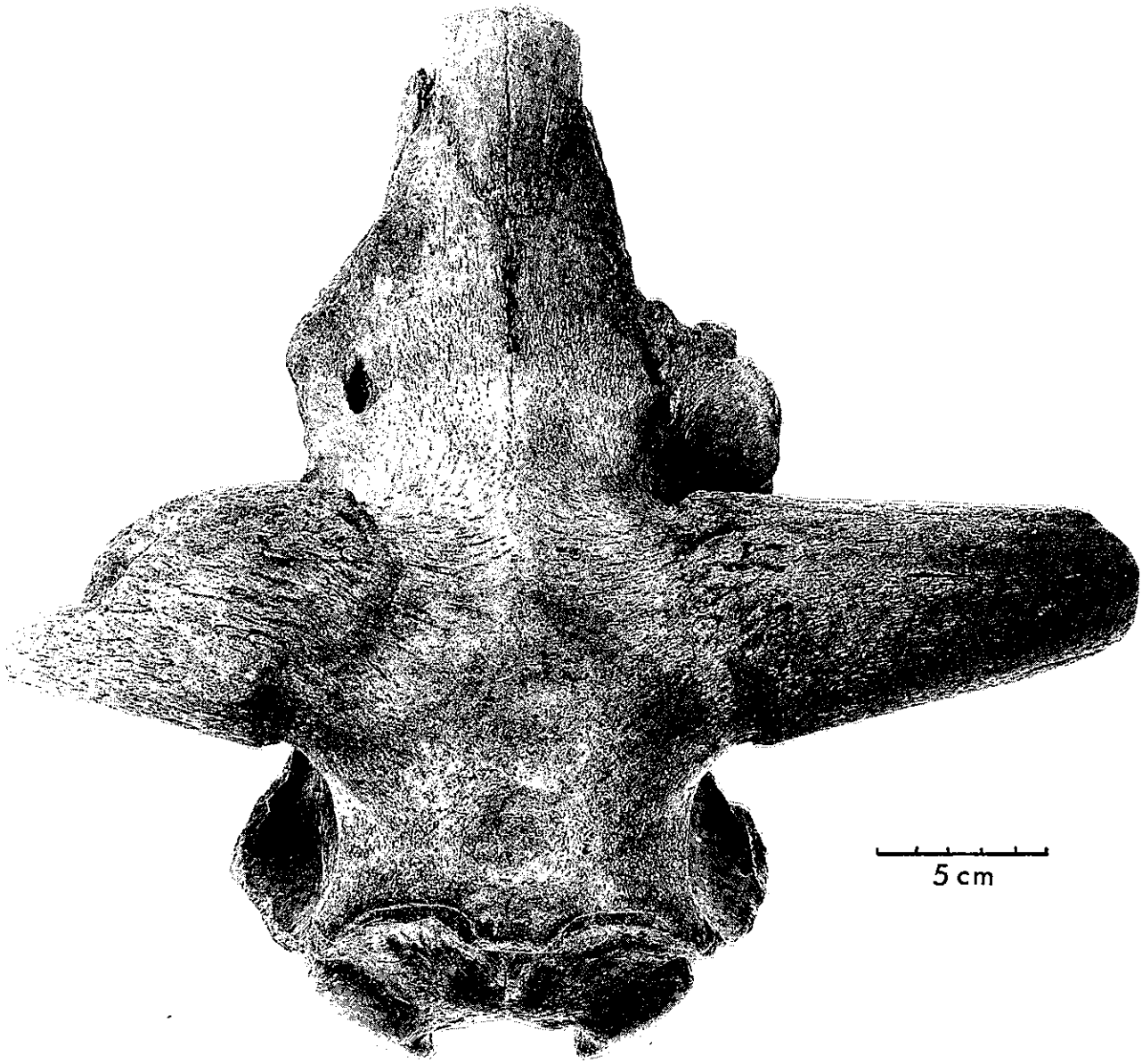

Figure 10. *Bootherium bombifrons* cranium, female (USNM 347315), Oregon Inlet, North Carolina; dorsal aspect.

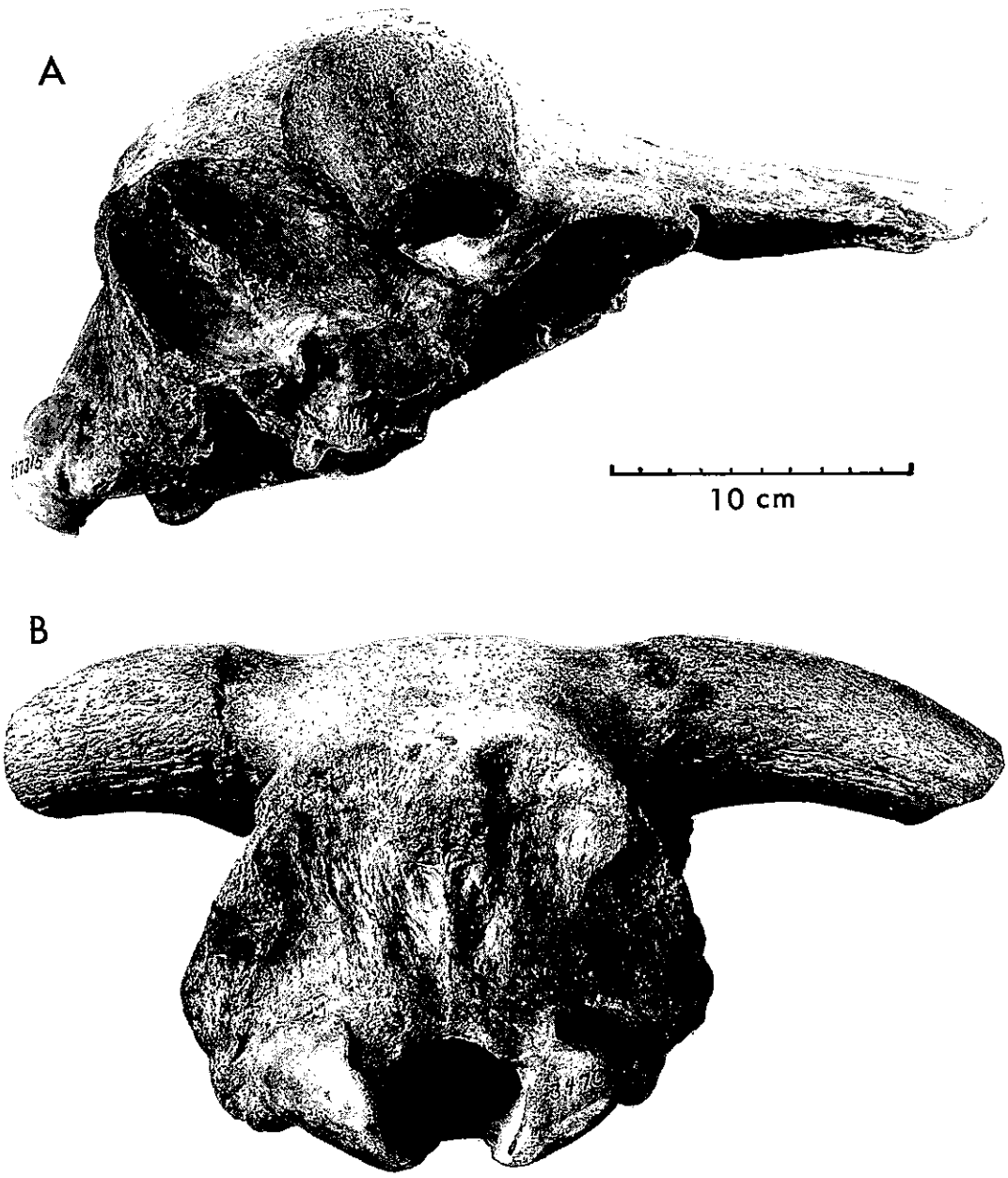

Figure 11. *Bootherium bombifrons* cranium, female (USNM 347315), Oregon Inlet, North Carolina; A, right lateral aspect, B, caudal aspect.

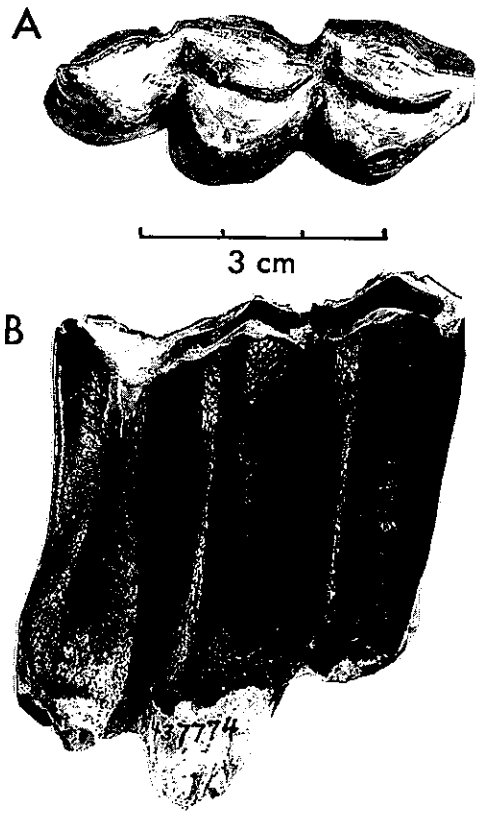

Figure 12. *Bootherium bombifrons* right m3 (USNM 437774), New Bern, North Carolina; A, occlusal aspect, B, labial aspect.

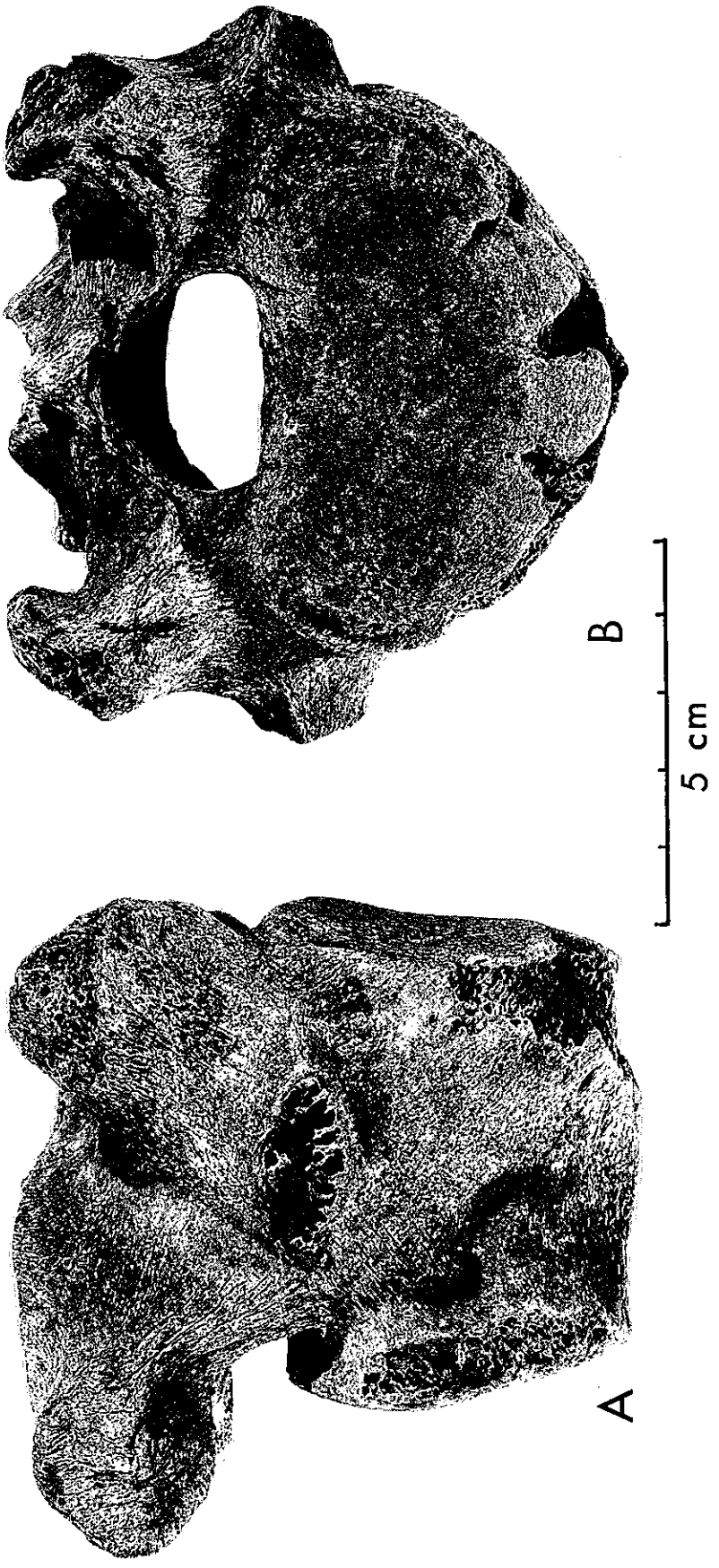

Figure 13. *Bootherium bombifrons* fifth lumbar vertebra (USNM 336108), Onslow Beach, North Carolina; A, right lateral aspect, B, rostral aspect.